Title: Light availability and land-use history drive biodiversity and functional changes in forest herb layer communities

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Abstract:

1. A central challenge of today's ecological research is predicting how ecosystems will develop under future global change. Accurate predictions are complicated by (i) simultaneous effects of different drivers, such as climate change, nitrogen deposition, and management changes; and (ii) legacy effects from previous land use.
2. We tested whether herb layer biodiversity (i.e. richness, Shannon diversity and evenness) and functional (i.e. herb cover, specific leaf area (SLA) and plant height) responses to environmental change drivers depended on land-use history. We used resurvey data from 192 plots across nineteen European temperate forest regions, with large spatial variability in environmental change factors. We tested for interactions between land-use history, distinguishing ancient and recent (i.e. post-agricultural) forests, and four drivers: temperature, nitrogen deposition, and aridity at the regional scale, and light dynamics at the plot-scale.
3. Land-use history significantly modulated global change effects on the functional signature of the herb layer (i.e. cover, SLA and plant height). Light availability was the main environmental driver of change interacting with land-use history. We found greater herb cover and plant height decreases and SLA increases with decreasing light availability in ancient than in recent forests. Furthermore, we found greater decreases in herb cover with increased nitrogen deposition in ancient forests, while warming had the strongest decreasing effect on the herb cover in recent forests. Interactive effects between land-use history and global change on biodiversity were not found, but species evenness increased more in ancient than in recent forests.
4. *Synthesis:* Our results demonstrate that land-use history should not be overlooked when predicting forest herb layer responses to global change. Moreover, we found that herb layer composition in semi-natural deciduous forests is mainly controlled by local canopy characteristics, regulating light levels at the forest floor, and much less by environmental changes at the regional scale (here: warming, nitrogen deposition and aridity). The observed disconnect between biodiversity and functional herb layer responses to environmental changes demonstrates the

importance of assessing both types of responses to increase our understanding of the possible impact of global change on the herb layer.

Keywords: atmospheric depositions, biodiversity measures, climate change, forest canopy features, functional signature, post-agricultural forests, resurvey, temperate deciduous forest, herb layer

Data availability statement: We intend to archive all data used in this paper on our public website: www.pastforward.ugent.be.

Introduction

Global environmental changes can strongly modify forest ecosystems and their plant communities (Gilliam et al., 2016; Hedwall et al., 2016; Perring et al., 2016). While there is already a good understanding of variation in plant community properties across spatial environmental gradients, knowledge of long-term temporal changes in ecosystems across environmental gradients remains limited (Amatangelo et al., 2014; Dwyer et al., 2014; Bjorkman et al., 2018). Understanding temporal changes in plant communities, and the role of global change, is complicated by the simultaneous effects of different drivers, such as climate change, atmospheric deposition of eutrophying and/or acidifying compounds, and management changes (Bernhardt-Römermann et al., 2015; Hedwall et al., 2016; Perring et al., 2018). In addition, legacy effects of past land use are often present in plant communities with slow dynamics (Perring et al., 2016; Bürgi et al., 2017). Hence, disentangling the combined and possibly interactive effects of land-use history and different environmental drivers on temporal community dynamics is key to predict how plant communities will be altered under future global change.

Plant communities can exhibit both biodiversity and functional changes in response to environmental change (Mayfield et al., 2010; Closset-Kopp et al., 2019). Assessing both types of changes is important to obtain a complete understanding of the impact of future global change on plant communities, especially as several studies report a disconnect between biodiversity and functional changes (Li et al., 2017; Perring et al., 2018). We focus our study on herb layer communities in temperate forests. The forest herb layer contains the majority of plant diversity (Gilliam, 2007) and plays a key role in forest functioning (Landuyt et al., 2019). Understanding how future environmental changes will affect the herb layer is key to make informed management decisions for sustaining forest biodiversity and functioning. We assessed changes in the functional signature of the herb layer, which represents a combination of functional ecological features at the community level. This was done through evaluating changes in the total herb layer cover, which can

123 be considered a measure for herb layer productivity. Several functions of the herb layer largely
124 depend on this productivity, including nutrient and carbon cycling, evapotranspiration and tree
125 regeneration (Landuyt et al., 2019). In addition, we evaluated changes in two important functional
126 traits (those properties that characterize the ecological strategies of species), i.e. plant height and
127 specific leaf area (SLA), which are both related to resource acquisition and expected to respond
128 strongly to environmental changes (Dubuis et al., 2013; De Frenne et al., 2015).

129 Global change drivers have the potential to alter herb layer communities by altering resource
130 availability and growing conditions at the forest floor that control herb layer community composition
131 (Landuyt et al., 2019). The simultaneous occurrence of different drivers, potentially causing
132 interactions, complicates understanding the magnitude and direction of shifts in resources and
133 conditions, and the consequent response of the herb layer community to these shifts. Here, we
134 focus on interactions between land-use history on the one hand, and ongoing environmental
135 changes (i.e. climate change, enhanced nitrogen deposition, and changing canopy cover and
136 composition) on the other hand. To account for land-use history, we compared post-agricultural
137 forests (further on referred to as 'recent forests') with ancient forests (i.e forest sites without any
138 known agricultural use, since at least 1810). We expect that alterations in resources and conditions
139 engendered by previous land use have steered communities and their constituent traits onto
140 trajectories of change, which may then be modulated by contemporary environmental changes
141 (Perring et al., 2016).

142 Although specific studies that consider land-use legacies when projecting the effects of multiple
143 environmental changes on future forest herb layer properties are rare, the literature provides
144 insights in the (interactive) effects of resource alterations as key agents of ecological change. In
145 general, the availability of water, nutrients and light will mainly determine the structure and
146 functioning of plant communities (Craine et al., 2012). Understanding the combined role of these
147 resources, and how land-use history and environmental changes simultaneously alter their

148 availability, can help to predict how plant communities will evolve under global change. For instance,
149 increased nitrogen (N) availability may promote plant growth in systems that have sufficient
150 phosphorus (P) (such as many post-agricultural forests), while it may not enhance plant growth in P-
151 limited systems (such as many temperate ancient forests (e.g. Gress et al., 2007)) (Hedwall et al.,
152 2017, although note Treseder et al., 2001). N deposition rates have a direct effect on N availability,
153 but warming and changes in light regimes can also affect N availability, as higher temperatures and
154 light levels can increase mineralization rates (Koch et al., 2007; Van Calster et al., 2007). Additionally,
155 climate change and altering light levels can affect the water availability through altering
156 evapotranspiration (Rind et al., 1990). Moreover, the drought-sensitivity of the system might
157 depend on the land-use history: forest sites without previous agricultural use (e.g. ancient forests)
158 typically have better developed organic soil layers than post-agricultural forest sites, improving their
159 water storage capacity, and thus their ability to mitigate the effects of a severe drought
160 (Greiffenhagen et al., 2006; Von Oheimb et al., 2014).

161 Resurvey data with a long time period (typically multiple decades) between surveys are ideally
162 suited to assess changes in systems that exhibit slower dynamics, such as plant communities in
163 temperate forests (Dornelas et al., 2013; Kapfer et al., 2017). In the present study, we use a
164 combined temporal and spatial approach to test for interactions between land-use history (i.e.
165 former agricultural use) and environmental changes (i.e. climate change, enhanced nitrogen
166 deposition, and changing canopy cover and composition) on biodiversity and functional changes in
167 temperate forest herb layer communities. We use herb layer resurvey data from 192 plots across
168 nineteen European temperate forest regions, where we can exploit large spatial variability in
169 environmental change factors (Verheyen et al., 2017). The timing of afforestation of the recent
170 forest sites ranged from 1810 to 1970, but with the majority (47/57) afforested before 1930. We
171 complement our resurvey study with direct characterisation of soil and canopy properties through *in*
172 *situ* measurements, which allows us to account for differences in soil type and canopy structure and
173 composition at the plot-scale in our analyses.

We tested the following hypothesis:

> The herb layer's biodiversity and functional signature will respond to environmental changes, but these responses depend on land-use history. When assuming that herb layer communities are mainly shaped by resource availability, we expect to see stronger herb layer responses to environmental changes in the recent forests, which are typically less P-limited due to former fertilization practices.

This hypothesis was based on two expectations, which we checked prior to testing our main hypothesis: (i) we expect that several decades after afforestation, legacies from former agricultural land use are mainly reflected in the soil nutrient levels, with higher phosphorus levels in recent forests due to former fertilization practices (Maes et al., 2019); (ii) we expect that differences in species pools due to dispersal limitations will be less important than nutrient availability in shaping herb layer communities, as the land-use change happened in the distant past and species already had time to colonize the recent forests.

Material and methods

Study sites

We selected 19 regions along spatial environmental gradients of atmospheric nitrogen deposition and climatic conditions (temperature, precipitation) within the European temperate deciduous forest biome (Fig. 1). The main selection criteria were the existence of prior understorey vegetation surveys (preferably at least 20 years ago, but we included one region with 17-19 year old vegetation data) and information on land-use history. In addition, we tried to minimize differences in parent material and topography between plots and regions. We aimed at maximizing differences in land-use history between plots within regions by sampling in ancient vs. recent forest, although this was not possible for all regions (Table 1). We define ancient forests as continuously forested since at least 1810, whereas recent forests have been afforested after 1810 (Hermy et al., 1999). Within the

57 recent forest plots, 31 plots were on former arable land, while 26 plots were on former grassland. Within fifteen out of nineteen regions, all, or all but one, plots were on the same soil type (Table 1). In addition, all plots are situated in 'mesic' forests, with a moderate supply of moisture (Table 1). All plots comprised closed-canopy forests with a variable tree and shrub layer composition, but we focused on plots predominantly composed of broadleaved species, although a higher occurrence of coniferous species in the easternmost regions with a hemiboreal climate was unavoidable. The canopies at the original survey consisted mainly of *Quercus robur/petraea* (104/192 plots), *Fraxinus excelsior* (67/192 plots), *Fagus sylvatica* (65/192 plots), *Carpinus betulus* (64/192 plots*)* in the tree layer and *Corylus avellana* (76/192 plots) in the shrub layer.

Data collection

In 2015 and 2016, we revisited 192 plots across 19 regions in temperate Europe that were established and surveyed at least 17 years ago (Fig.1, Table 1). The year of the original survey varied between 1928 and 1998 (Table 1). Depending on the region, plot relocation was based on one or more of the following properties: permanent markings in the field, GPS coordinates, physical maps, plot descriptions, drawings, photographs, and the original composition of the canopy layer (Appendix A). Plots were either rectangular or circular, and varied in size between 50 and 2500 m^2 (Table 1). To assure comparability between our survey and the original survey, we followed the original definitions of the vegetation layers, which differed among regions (Appendix B). A vegetation survey comprised a division of all vascular plants into three layers: herb layer, shrub layer and tree layer. The herb layer typically comprised all herbaceous species and the woody species (e.g. tree and shrub seedlings) below a threshold ranging from 0.25 to 1.3 m (threshold differed between regions; see Appendix B). For each layer, we visually estimated the cover (%) of each species, as well as the total cover of the layer. When cover values of the old survey were reported in different cover-abundance scales (e.g. Braun-Blanquet, 1964), we converted these to percentages (Appendix B).

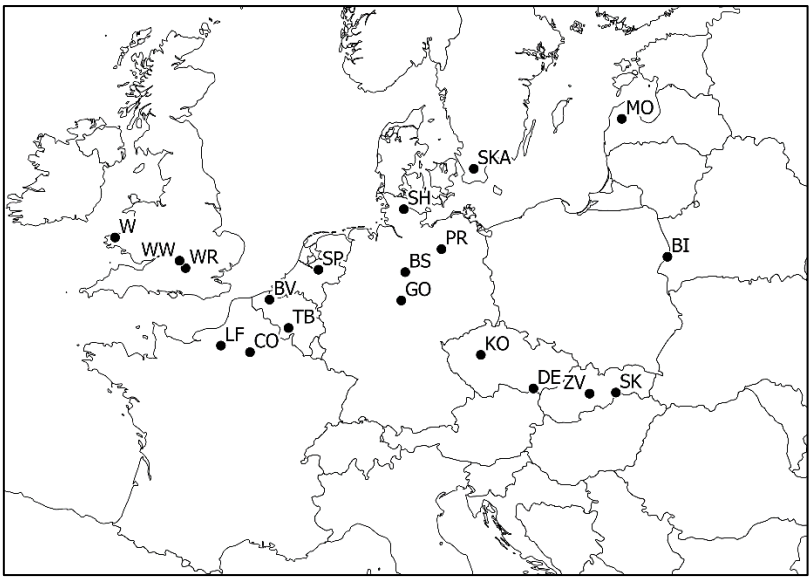


Figure 1. Geographical distribution of the 19 forest regions where vegetation surveys were performed (the labels refer to Table 1)

In addition to vegetation surveys, we collected samples of the mineral topsoil in each plot (a composited sample from five locations within the plot). We analysed the 0–10 cm samples for pH_{KCl}, proportion of exchangeable base cations, total and Olsen phosphorus (P) concentration (mg kg^{-1}), organic and inorganic carbon (C) and total nitrogen (N) concentration (%), and soil organic matter (%), and the 10–20 cm samples for soil texture (% Clay, % Silt, % Sand). We also collected a 0-10 cm soil sample with a Kopecky ring at the centre of each plot to determine the whole-soil bulk density (see Maes et al. (2019) for further details on soil analyses and properties).

Response variables

We derived six plant community descriptors for both the plots in the old (o) and new (n) surveys. To assess the biodiversity of the herb layer, we used **species richness (*SR*)**, **Shannon diversity (*DIV*)**, and **species evenness (*EVEN*)**. Species richness is the number of species present within the plot. Shannon diversity is a combined measure of species richness and evenness, which weights species by their abundance (Shannon, 1948). Species evenness is the distribution of abundance among species. It ranges from zero to one, with one representing a perfectly equal distribution of all occurring species.

We followed Smith & Wilson (1996) to calculate evenness based on the variance in species' abundances (see Appendix C for details).

To assess the functional composition of the herb layer, we used community weighted mean (CWM) values for the two traits **'plant height' (*height)*** and **'specific leaf area' (*SLA*)**, and the **total cover of the herb layer species (*COVER*)**. We gathered trait data from different databases including LEDA (Kleyer et al., 2008) (Appendix D). The total herb cover is the sum of the visually estimated cover of each species in the herb layer. Each response variable was based on the 'strict' herb layer, containing only the herbaceous species, and excluding seedlings and shrub species for three reasons: (i) tree and shrub species do not remain structurally part of the herb layer throughout their life cycle, (ii) many recorded trait values are representative for adult trees, shrubs and climbers and not the juvenile state found in the understorey, and (iii) seedlings were not always included in the original surveys (see Appendix E for species lists). Nomenclature was standardized manually based on The Plant List (2013).

We used the change in community descriptors between surveys as response variables, calculated as response ratios (RR):

$$RR_X = \frac{\ln(\frac{X_n}{X_o})}{\Delta t} \quad (1)$$

where X is one of the community descriptors, 'n' and 'o' refer to the new and old survey, and Δt is the number of years between surveys. These response ratios are further denoted as RR_{SR}, RR_{DIV}, RR_{EVEN}, RR_{HEIGHT}, RR_{SLA} and RR_{COVER}.

To improve our understanding of what could be driving the changes in these six main response variables, we evaluated the changes (again calculated as log response ratios) in two additional variables related to the herb layer composition: the proportion (%) of the herb layer cover occupied by (i) forest specialists (RR_{FS}) and (ii) graminoids (RR_{GRAM}). Forest specialists are the species most strongly associated to closed forests, following Heinken (2019) (Appendix F).

Explanatory variables

Site conditions

We included **land-use history (LUH)** as a categorical variable, distinguishing plots in ancient forest (forested since at least 1810) and recent forest (former arable land/grassland forested after 1810) (Table 1). **Soil type** was also a categorical variable with three groups, obtained with cluster analysis based on soil texture (% Clay, % Silt, % Sand) and carbonate or inorganic carbon concentration (%) (see Maes et al. (2019) for details of this analysis). 'ClayCarbonate' soils represent silty-clay-carbonate soils with high inorganic carbon concentration and high pH_{KCl}, but low C/N-ratio and litter mass (i.e. faster mineralization). The 'ClayNoCarbonate' soils represent silty-clay soils without the presence of carbonates (low inorganic carbon concentration) and intermediate pH_{KCl}, C/N-ratio and litter mass. The 'Sand' soils represent poor sandy soils with a low inorganic carbon concentration and high C/N-ratio and litter mass reflecting higher acidity and lower nutrient concentration (Table 1).

Since **Olsen P** was not correlated with the soil type groups, and because it is an important nutrient for plant growth that is expected to be affected by past land use (De Keersmaeker et al., 2004), we included the Olsen P concentration (mg kg^{-1}) measured at the new survey as a separate predictor (Maes et al., 2019). We expected soil moisture to affect community traits (Schaffers et al., 2000) and therefore included a community weighted mean **Ellenberg Indicator Value score for soil moisture (EIV_F)** from the plot's herbaceous community at the old survey (Table 1). EIVs for moisture range from 1 (species occurs on dry soils) to 9 (species occurs on wet soils) (Diekmann, 2003).

Lastly, we included **plot size** (m^2) (Table 1) as an explanatory variable. We expect plot size to affect community property changes as larger plots have more chance of including infrequent species, which may also be more likely to appear or disappear between surveys.

Plot-scale drivers of change

At the plot-level, we expect changes in the cover and composition of the canopy (including both shrub and tree layer) to be the main driver of changes in the herb layer community. Canopy changes

between surveys can be the result of changes in the type and intensity of forest management, successional trajectories of the forest canopy and natural disturbances. We included the response ratios (see Equation 1) of the **canopy cover (RR_{CC}),** the **canopy's shade-casting ability (RR_{SCA})** and the **litter quality (RR_{LQ})** as explanatory variables in our analysis. To calculate the overall canopy cover, we combined cover estimates of all species in the tree and shrub layer using the formula developed by Fischer (2015), which accounts for overlap between species and between layers. We calculated the shade-casting ability (SCA) and litter quality (LQ) as a cover weighted average of, respectively, ordinal SCA and LQ scores (listed in Appendix G), ranging between 1 (very low SCA and very low decomposition rate, respectively) and 5 (very high SCA and very high decomposition rate, respectively) (see also Van Calster et al., 2008; Verheyen et al., 2012).

Across all regions, both SCA and litter quality increased significantly, while canopy cover did not change (Appendix H). We expected these canopy variables (SCA, litter quality and cover) to be related to management changes, and checked this through assigning a 'management change category' to each plot (Table 1, Appendix I), based on management history data obtained via local experts. Only the changes in canopy cover clearly differed among the management intensity categories, with the strongest canopy cover increases where management intensity decreased (Appendix I). Inspection of the changes in frequency and cover of the ten most frequent tree and shrub species in the new survey revealed that the increasing importance of shade-casting species is mainly due to the increases of *Acer pseudoplatanus, Carpinus betulus* and *Fagus sylvatica*. The increased litter quality is mainly related to increases of *Acer campestre* (Appendix H). These four tree species are all shade tolerant late successional species, which indicates that SCA and litter quality increases are probably related to processes of natural succession with time.

Regional-scale drivers of change

At the regional scale, we were interested in the effect of two global climatic drivers and a eutrophication driver on the herb layer composition. We calculated the rate of change of **mean annual**

temperature (ΔMAT) and **De Martonne aridity index (ΔAridity)** as the difference between the new and the old survey, divided by the number of years between surveys. To derive the mean annual temperature and aridity index at both survey times, we averaged annual values for the 10 years preceding the survey (as per Bernhardt-Römermann et al. (2015); Perring et al., (2018)). We extracted temperature and precipitation data from the Climate Research Unit (CRU TS v. 4.02; 0.5° resolution) (Harris et al., 2014). The De Martonne aridity index is one of the best known and widely used aridity indices in applied climatology (Croitoru et al., 2013; Hrnjak et al., 2014), and is calculated as follows (De Martonne, 1925):

$$\mathrm{Aridity_{DM}} = \frac{\mathrm{Prec}}{\mathrm{MAT} + 10} \qquad (2)$$

with 'MAT' the mean annual temperature (°C) and 'Prec' the annual amount of precipitation (mm). A lower value of $\mathrm{Aridity_{DM}}$ represents drier conditions. The mean annual temperature increased in all regions in between surveys, with an average increase of 0.026°C (± 0.002) per year across all regions (Table 1). The De Martonne aridity index increased in some and decreased in other regions, with no significant overall trend across regions (Table 1).

We compiled data on nitrogen (N) deposition for the year 2000 from the EMEP database (http://www.emep.int), which allows deposition data for the whole of Europe to be derived with a resolution of 50 km x 50 km. We applied correction factors from Duprè et al. (2010) to obtain N deposition values for each year in between surveys, and then calculated the average annual rate of **nitrogen deposition (Ndep)** as the total amount of N deposition in between surveys divided by the number of years between surveys. We used the mean value across plots per region for each global change driver for our analyses. The average N deposition rate between surveys was 15.70 kg N ha^{-1} (± 1.22) per year (Table 1).

Statistical analysis

We performed all statistical analyses and visualizations in R version 3.6.0 (R Core Team, 2019) with the packages 'vegan', 'nlme', 'MuMIn', 'ggplot2', and 'sjPlot' (Barton, 2019; Lüdecke, 2019; Oksanen et al., 2019; Pinheiro et al., 2019; Wickham et al., 2019).

To check our expectation that initial species pools (at the time of the first survey) between ancient and recent forests were similar, we conducted a permutational multivariate analysis of variance (PERMANOVA) using Bray-Curtis dissimilarities with 999 permutations (based on abundance data; Bray and Curtis (1957)). We visualized the compositional differences in the herb layer with nonmetric multidimensional scaling (NMDS). Species pools at the original survey time were indeed similar for ancient and recent forests in most regions. We only found significantly different species pools in two regions (Skåne and Wales) (Appendix J).

To check our expectation that Olsen P concentrations differed between ancient and recent forest plots, we performed linear mixed-effect modelling, including land-use history as a fixed effect and region as a random effect. Overall, Olsen P concentrations were significantly higher in recent forests than ancient forests ($p = 0.046$) (Appendix K), but there were unexpected trends for some regions (Tournibus, Wales and Wytham Woods), with higher Olsen P levels in ancient than recent forests (although not significant). These regions with unexpected patterns in P soil concentrations are characterised by a low P nutrient supply in agriculture (Bomans et al., 2005), so that we can assume a low agricultural intensity in these regions.

We used linear mixed-effect modelling to test which explanatory variables are significantly affecting the chosen response variables. We standardized (scaled and centred) all continuous explanatory variables prior to analysis to enable comparison of their effect sizes. We applied a logarithmic transformation on 'Olsen P' and 'Plot size' to improve normality. To detect possible multicollinearity among the explanatory variables, we calculated variance inflation factors (VIF) according to Zuur et al. (2009). VIF values were very low (<2), indicating low collinearity.

For each response variable, we fitted a linear mixed-effect model with the following explanatory variables as fixed effects (see '*Explanatory variables'* for abbreviations):

$$\text{Response variable} \sim \text{LUH} + \text{Soil type} + \ln(\text{Olsen P}) + EIV_F + \ln(\text{Plot size}) + RR_{CC} + RR_{SCA} + RR_{LQ} + \Delta\text{MAT} + \Delta\text{Aridity} + \text{Ndep} + \text{LUH}:RR_{CC} + \text{LUH}:RR_{SCA} + \text{LUH}:RR_{LQ} + \text{LUH}:\Delta\text{MAT} + \text{LUH}:\Delta\text{Aridity} + \text{LUH}:\text{Ndep} + (1|\text{Region}) \quad (3)$$

where '(1|Region)' represents the inclusion of a random effect term 'region' with varied intercepts only to account for the hierarchical structure of the data. We also incorporated 'region' as a weights term, i.e. we controlled for heterogeneity in residual spread. With ANOVA, we confirmed that both the random effect term and the weights term significantly (alpha = 0.05) improved the model for each response variable. All models were fit with restricted maximum likelihood (REML). We found no clear patterns in the residuals for each model, based on graphical evaluation (Zuur et al., 2009). We report estimates and 95% confidence intervals for each explanatory variable in each model. We calculated the marginal and conditional R^2 for each fitted model, representing the variance explained by fixed factors and the variance explained by both fixed and random factors, respectively (*MuMIn* package; Nakagawa et al., 2013).

Table 1. Ecological details of the 19 regions where we did vegetation resurveys. Δt = time interval between original and new survey (in years); LUH = land-use history; AF = ancient forest; RF = recent forest; EIV-F = Ellenberg indicator value for soil moisture; S = Sand; ClayC = Clay with carbonates; ClayNC = Clay with no carbonates; ΔMAT = rate of change of mean annual temperature; ΔAridity = rate of change of De Martonne aridity index; Ndep = average annual rate of nitrogen deposition; se = standard error. ΔManagement indicates in how many plots management intensity has decreased (↓), increased (↑) or stayed the same (=) over time (Appendix I). See text for a detailed description of the variables. For ΔMAT, ΔAridity and Ndep, mean values ± standard error across all regions are shown at the bottom of the table, as well as a p-value to indicate whether the mean value is significantly different from zero.

ID	Region, Country	Δt (y)	LUH (135 AF, 57 RF)	Plot size (range) m^2	Mean Olsen P (range) mg kg^{-1}	Mean EIV-F (range)	Soil type	ΔMAT °C y^{-1}	ΔAridity mm °C^{-1} yr^{-1}	Ndep kg ha^{-1} y^{-1}	ΔManagement (112↓, 65=, 15↑)
BI	Bialowieza, PL	31-50	15 AF	50-400	36 (10.4-100.5)	5.4 (5.1-6.0)	S	+0.029	-0.028	13.75	10 =, 5 ↓
BS	Braunschweig, GE	24-25	5 AF, 5 RF	625	33.3 (5.7-82.8)	5.1 (4.7-5.6)	S	+0.035	-0.101	17.22	4 =, 6 ↓
BV	Binnen-Vlaanderen, BE	35	4 AF, 5 RF	150	34.1 (10.8-53.3)	6.0 (5.5-6.4)	S(8), ClayC(1)	+0.033	+0.069	22.12	5 =, 4 ↓
CO	Compiègne, FR	47	10 AF	200-2000	17.6 (6-40.6)	5.1 (4.5-6.0)	S	+0.026	-0.015	15.66	5 =, 5 ↓
DE	Devin, CZ	52-62	3 AF, 7 RF	100-600	34.4 (10.2-75.3)	4.6 (3.7-6.2)	ClayC(5), ClayNC(5)	+0.024	-0.028	16.45	10 ↓
GO	Göttingen, GE	48-60	10 AF	100-400	14.3 (6.6-53.4)	5.5 (5.1-5.9)	ClayC(6), ClayNC(4)	+0.017	-0.010	17.75	7 =, 3 ↓
KO	Koda, CZ	58	10 AF	400	28.7 (7.7-58.6)	4.6 (4.3-4.9)	ClayC(1), ClayNC(9)	+0.021	+0.003	16.32	3 =, 7 ↓
LF	Lyons-la-forêt, FR	43	10 AF	300-1000	15.5 (10.2-26.9)	5.3 (5.0-5.7)	ClayNC(9), S(1)	+0.030	-0.030	16.23	10 ↑
MO	Moricsala, LV	88	5 AF, 3 RF	1250-2500	11.4 (6.4-26.4)	5.0 (4.6-5.4)	ClayNC(1), S(7)	+0.013	+0.008	5.2	7 =, 1 ↓
PR	Prignitz, GE	17-19	5 AF, 5 RF	120-300	19.3 (7.3-32.8)	5.6 (5.1-6.0)	S	+0.030	-0.042	16.33	5 =, 5 ↓

SH	Schleswig-Holstein, GE	29-31	5 AF, 5 RF	64-400	37.9 (9.7-154.9)	5.1 (4.9-5.3)	S	+0.045	-0.050	18.68	10 =
SK	Slovak Karst, SK	32-40	10 AF	500	10.9 (3.5-49)	4.8 (4.5-5.0)	ClayNC	+0.024	-0.037	11.57	10 ↓
SKA	Skåne, SW	31	8 AF, 2 RF	500	30.4 (9.6-95)	5.3 (4.7-5.8)	ClayNC(6), S(4)	+0.026	+0.080	12.88	4 =, 6 ↓
SP	Speulderbos, NL	57-59	5 AF, 5 RF	100	52.7 (24.9-92)	5.2 (5.0-6.0)	S	+0.019	-0.009	31.11	4 =, 6 ↓
TB	Tournibus, BE	48	5 AF, 5 RF	100	11.8 (6.3-24)	5.3 (4.6-5.9)	ClayNC	+0.027	-0.092	18.6	10 ↓
W	Wales, UK	45	5 AF, 5 RF	200	44.2 (18.3-91.1)	5.8 (5.2-6.4)	ClayNC	+0.018	+0.088	8.93	10 ↓
WR	Warburg Reserve, UK	41	5 AF, 5 RF	100	19.5 (14.2-23.7)	5.4 (4.9-5.8)	ClayC(9), ClayNC(1)	+0.025	+0.026	15	5 =, 5 ↓
WW	Wytham Woods, UK	41	5 AF, 5 RF	100	13.2 (6.7-19.9)	6.0 (5.3-6.3)	ClayNC(7), S(3)	+0.022	+0.032	12.39	5 ↓, 5 ↑
ZV	Zvolen, SK	51-52	10 AF	500	35.5 (6.5-111.7)	4.7 (4.2-5.2)	ClayNC	+0.024	-0.027	12.64	1 =, 9 ↓
								Mean ± se across regions:			
								+0.026 ± 0.002 (p<0.001)	-0.009 ± 0.012 (p = 0.47)	15.70 ± 1.22 (p<0.001)	

384

385

386 **Results**

387 *Biodiversity and functional changes*

388 For species richness and Shannon diversity, we observed significant increases or decreases over time
389 in a few regions, but no overall trend across the regions (Fig. 2A and 2B). Species evenness on the
390 other hand, increased significantly across all regions, with decrease observed only in one region (Fig.
391 2C). The total cover of the herb layer decreased significantly between surveys in 14 out of 19 regions
392 and across all regions (Fig. 2D). We found no significant temporal trends across regions for the
393 community weighted mean trait values of plant height and specific leaf area (SLA) (Fig. 2E and 3F),
394 although it seems that for plant height, the lack of an overall trend is mainly caused by one region
395 (Warburg Reserve) (Fig. 2A). Excluding the plots in Warburg Reserve from the dataset resulted in an
396 overall significant increase in plant height across regions. The response ratio of species richness was
397 positively correlated with both the response ratio of Shannon diversity ($r_s = 0.71$; $p < 0.001$) and total
398 herb cover ($r_s = 0.53$; $p < 0.001$). The response ratios of evenness and total herb cover were negatively
399 correlated ($r_s = -0.67$; $p < 0.001$) (see Appendix L for overview of correlations between response
400 variables).

401 *Potential (interactive) drivers of biodiversity and functional changes*

402 We found no significant interactive effects for the three biodiversity measures (Fig. 3). Olsen
403 phosphorus (P) was the only significant predictor for both the changes in species richness (RR_{SR}) and
404 Shannon diversity (RR_{DIV}), with a positive effect on both response variables (Fig. 3). For the changes in
405 species evenness (RR_{EVEN}), we found that land-use history and the shade-casting ability (RR_{SCA}) of the
406 canopy were significant predictors. The response ratio of species evenness was higher in ancient
407 forests than in recent forests, and in plots with a higher response ratio of the canopy's shade-casting
408 ability (Fig. 3).

For the change in the total herb cover (RR_{COVER}), we found significant interactive effects between land-use history and four drivers of change, i.e. the rate of N deposition (Ndep) ($p < 0.001$), the rate of change in mean annual temperature (ΔMAT) ($p = 0.006$), the response ratio of canopy cover (RR_{CC}) ($p = 0.006$), and the response ratio of shade-casting ability (RR_{SCA}) ($p = 0.015$) (Fig. 3). In *ancient* forests, the response ratio of the total herb cover (RR_{COVER}) was negatively affected by Ndep, RR_{CC} and RR_{SCA} (Fig. 4A, 4C and 4D), but it was not affected by ΔMAT (Fig. 4B). In *recent* forests, Ndep, RR_{CC} and RR_{SCA} had no or a slightly positive effect on RR_{COVER} (Fig. 4A, 4C and 4D), while ΔMAT had a negative effect on RR_{COVER} (Fig. 4B).

For the change in community weighted mean plant height (RR_{HEIGHT}), we found significant interactive effects between land-use history and the response ratio of canopy cover (RR_{CC}) ($p < 0.001$) (Fig.3). In *ancient* forests, RR_{CC} had a negative effect on RR_{HEIGHT}, while no clear effects were found in *recent* forests (Fig. 4E).

For the change in community weighted mean SLA (RR_{SLA}), we found significant interactive effects between land-use history and the response ratio of canopy cover (RR_{CC}) ($p = 0.020$), the response ratio of shade-casting ability (RR_{SCA}) ($p = 0.001$) and ΔAridity ($p = 0.045$) (Fig. 3). In *ancient* forests, RR_{CC} and RR_{SCA} had a positive effect on RR_{SLA}. In *recent* forests, RR_{CC} had no effect on RR_{SLA}, and RR_{SCA} had a negative effect on RR_{SLA} (Fig. 4F and Fig. 4G). Differences in RR_{SLA} responses to ΔAridity between ancient and recent forests were very minor (Fig. 4H), and therefore, this only just significant interactive effect will not further be discussed.

The amount of variation explained by the model (reflected by marginal R^2 (R^2m) values; Fig.3) was low for the response ratios of species richness (0.16), Shannon diversity (0.11), species evenness (0.13) and total herb cover (0.17), but quite high for the response ratios of the functional traits 'height' (0.41) and 'specific leaf area' (0.30). The conditional R^2 (R^2c) was generally much higher than R^2m (see Fig. 3), indicating that much of the variation in the response variables can be explained by the random effect term 'region'.

Forest specialists and graminoids

Across all regions, both the proportion of forest specialists (FS) and graminoids (GRAM) did not significantly change between surveys. RR_{FS} increased with increasing canopy cover, but *only* in ancient forests, while no relation was found in recent forests. RR_{GRAM} decreased with higher Olsen P and decreased with higher Ellenberg indicator values for soil moisture (Appendix F).

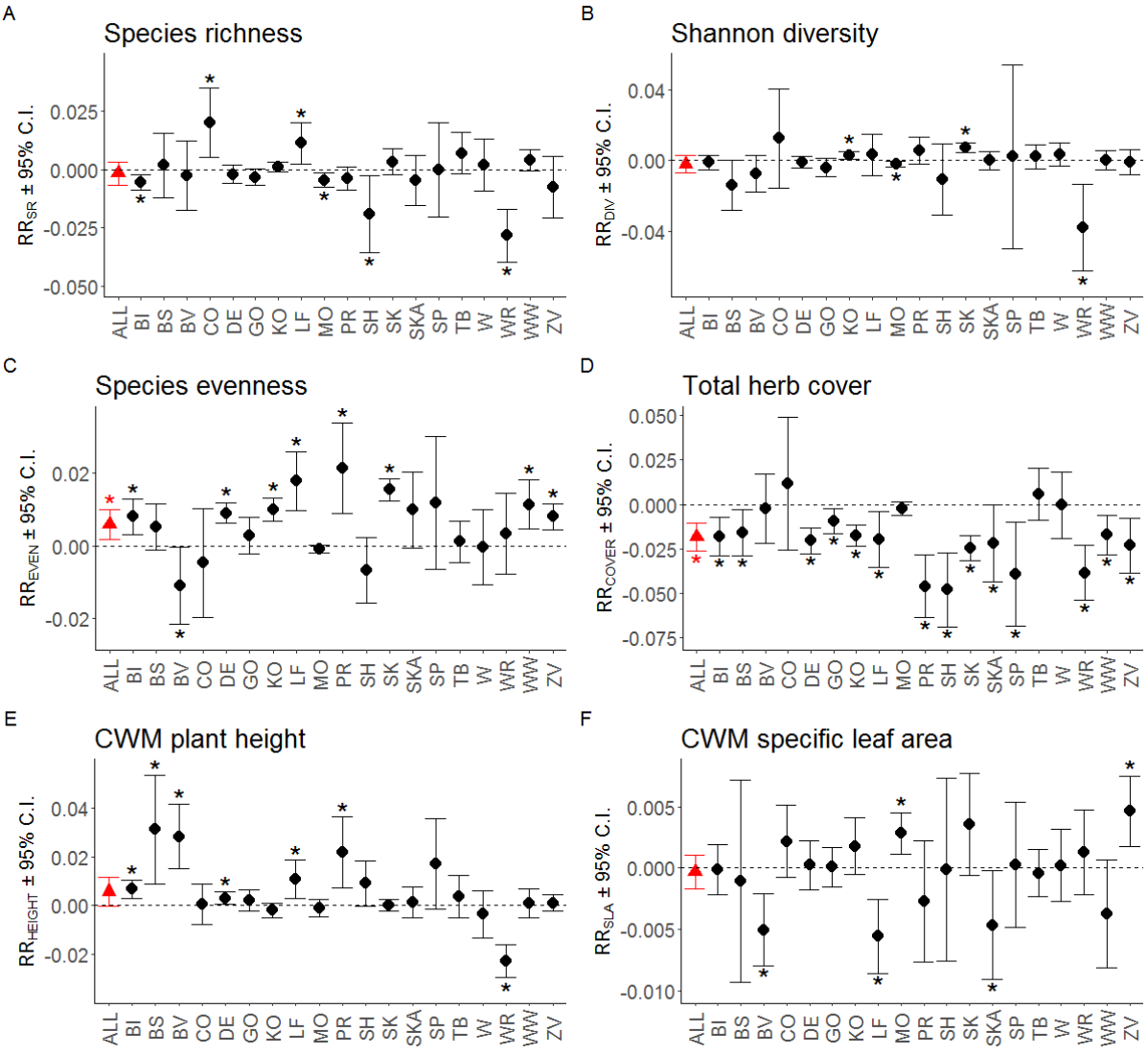
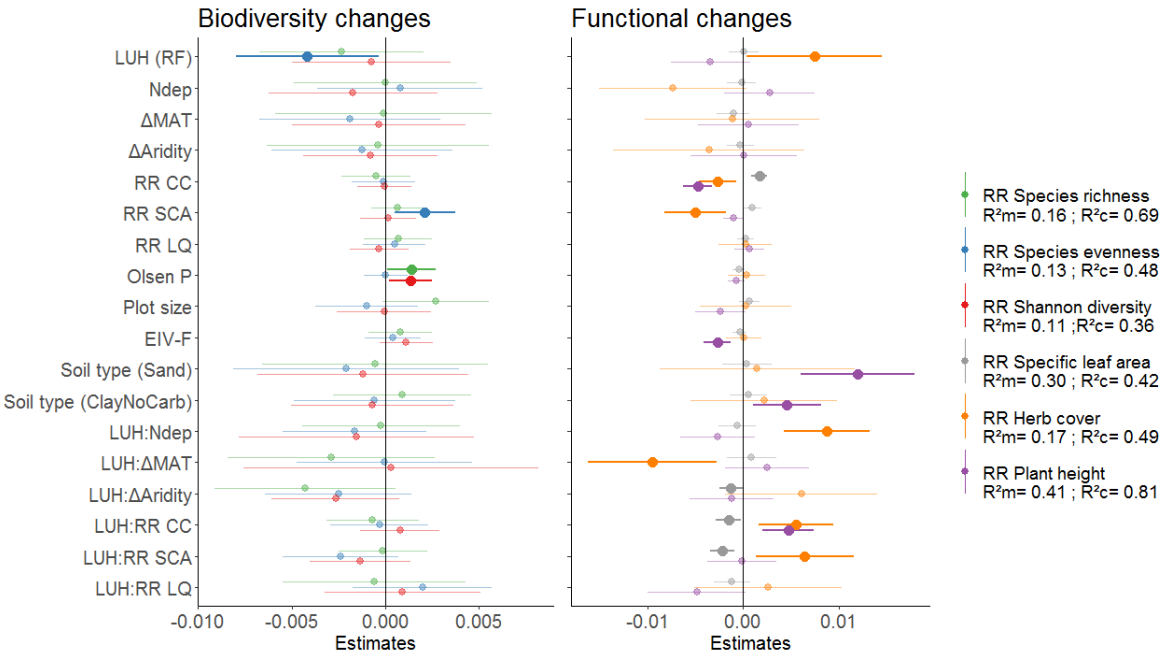


Figure 2. Temporal shifts in observed: species richness (SR) (A), Shannon diversity (DIV) (B), species evenness (EVEN) (C), total herb layer cover (COVER) (D), community-weighted mean (CWM) plant height (HEIGHT) (E) and community-weighted mean (CWM) specific leaf area (SLA) (F) across all regions (red triangle) and for the 19 regions separately (black dots). Mean (± 95 % confidence interval) log response ratios ($RR = \ln(X_{new}/X_{old})/\Delta t$)

444 are shown based on the observed plot values in the old (X_{old}) and new (X_{new}) survey. '*' indicates a significant

445 change, with confidence intervals excluding zero. The region labels refer to Table 1.



446

447 **Figure 3.** Estimates and 95% confidence intervals for each explanatory variable in the six models that were

448 fitted for the six different response variables listed in the legend. Non-significant effects (with confidence

449 intervals including zero) are transparent. Marginal R^2 (R^2m) and conditional R^2 (R^2c) of each model are

450 provided in the legend. RR = log response ratio (ln (X_{new}/X_{old})/Δt); LUH = land-use history; RF = recent forest;

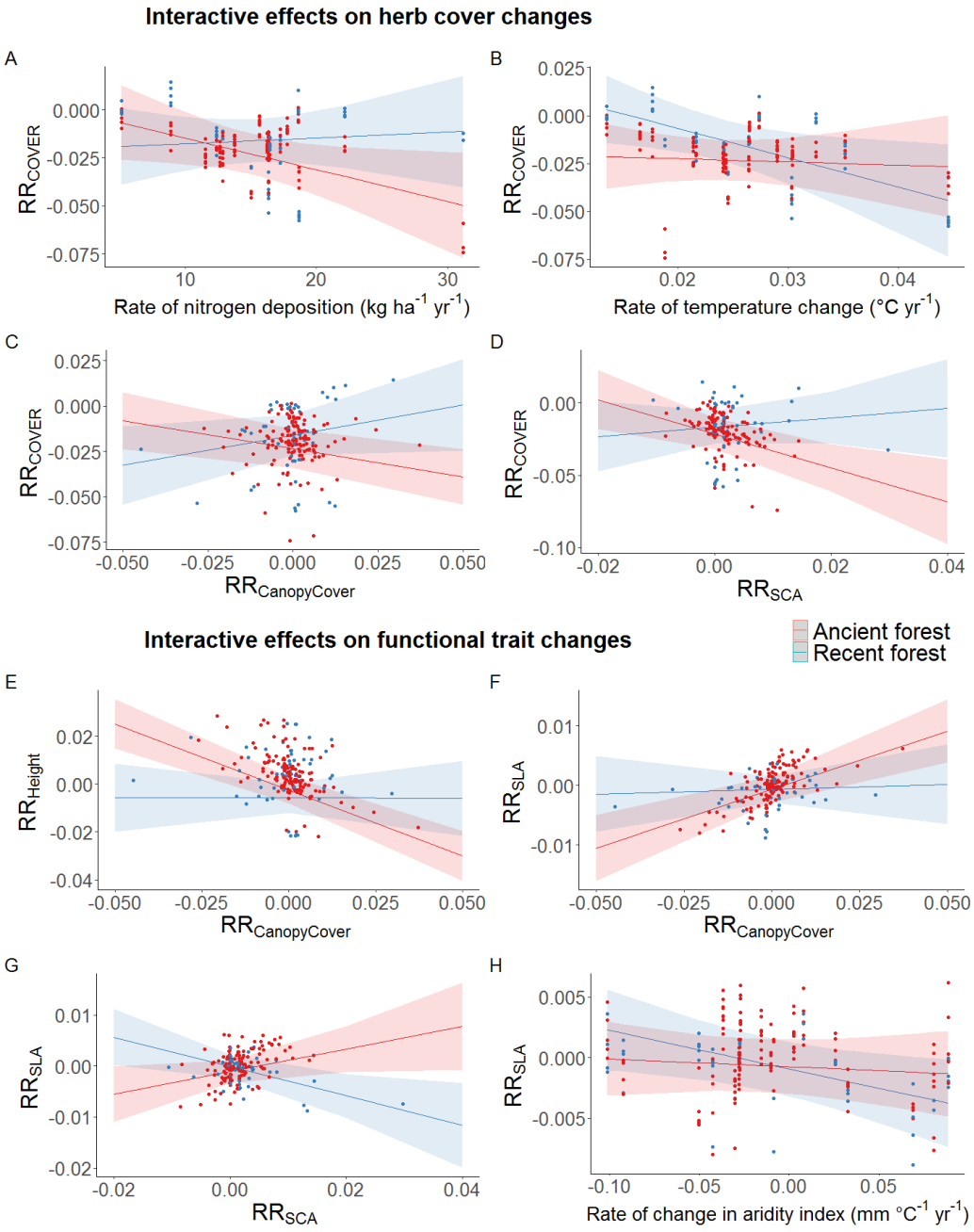
451 Ndep = nitrogen deposition; MAT = mean annual temperature; CC = canopy cover; SCA = shade-casting ability

452 of the canopy; LQ = litter quality; EIV-F = Ellenberg indicator value for soil moisture. See appendix M for table

453 with full model results.

454

455



456

457 **Figure 4.** Interactive effects on total herb cover change (RR_{COVER}) (A-D) between land-use history and rate of
458 nitrogen deposition (A), rate of change in mean annual temperature (B), canopy cover change ($RR_{CanopyCover}$) (C)
459 and shade-casting ability change (RR_{SCA}) (D). Interactive effects on community-weighted mean (CWM) plant
460 height change (RR_{HEIGHT}) between land-use history and canopy cover change (E). Interactive effects on CWM
461 specific leaf area (SLA) change (RR_{SLA}) (F-H) between land-use history and canopy cover change (F), shade-
462 casting ability change (G), and De Martonne aridity index change (H). Fitted values (dots) and average model
463 estimates of the effects (full lines) with 95% confidence intervals (shading), in which the values of the other

continuous variables were set at their observed mean and the factor 'soil type' was set at its reference level ('ClayCarb'), are shown.

Discussion

Our results confirmed the first part of our hypothesis, i.e. biodiversity and functional herb layer responses to environmental changes depend on land-use history. The second part of our hypothesis, i.e. herb layers in recent forests respond more strongly to environmental changes likely because of higher phosphorus availability, was only confirmed for warming, which mainly affected the herb cover in recent forests. In contrast, ancient forest herb layers were more sensitive to decreased light availability and increased nitrogen deposition than recent forests. Overall, light availability seemed to be the main factor controlling herb layer changes over time. Not only differences in P levels, but also differences in the canopy's shade-casting ability between ancient and recent forests played a key role in explaining the dependencies of the herb layer responses on land-use history.

Land-use history and light availability interactions drive biodiversity and functional responses of the herb layer

Across our study regions, the total cover of the herb layer decreased over time, likely indicating lower understorey biomass production, which can affect several functions of the understorey, such as nutrient cycling through decreased retention of nutrients (Landuyt et al., 2019). Petzold et al. (2018) attributed their findings of decreased herb cover to a reduced management intensity. In ancient forests, our findings conform with Petzold et al. (2018), as increasing canopy cover due to reduced management intensity, as well as increasing shade-casting ability resulted in a decrease in total herb cover, which can be explained by a lower light availability. Surprisingly, in recent forests, stronger increases in cover and shade-casting ability of the canopy seemed to have no effect on cover changes of the herb layer, or even slightly reduced the intensity of cover decline.

In the ancient forests, we could relate the stronger decreases in herb cover with increasing canopy cover to an increase in the share of forest specialists (Heinken, 2019) in the community (Appendix F).

Hence, herb cover losses in ancient forests were mainly caused by the disappearance of species that typically occur in forest openings and cannot withstand very dark closed forest conditions. This observation is in accordance with findings of Penone et al. (2019), who found a negative effect of increased canopy cover on vascular plant abundance in the understorey, but a positive effect on specialisation. In the recent forests however, there were no clear shifts in the share of 'closed forest species' with increasing canopy cover or shade-casting ability. Hence, those species that disappeared in the ancient forest plots that became darker seemed to survive in recent forest plots despite the increased shade levels, suggesting that nutrient availability can alter plant species responsiveness to light availability. Ellenberg (1939) already showed that many herb layer species need a higher nutrient supply to compete successfully with other species under darker conditions. Also Heinken (1995) observed an interaction between nutrient and light availability on the herb layer cover, with nutrient-rich sites having similar herb cover, regardless of light availability, while nutrient-poor sites had much lower cover values under darker conditions. In a recent study, Gilliam (2019) also demonstrated the interaction between nutrient and light availability in the herb layer of temperate forests, where he found that increased nutrient availability caused a shift in factors controlling herb layer dynamics from variation in soil resources to variation in canopy structure.

The idea that the shade-tolerance spectrum of plants is wider on nutrient-rich sites than on nutrient-poor sites was also suggested by Coomes et al. (2009), and is consistent with the hypothesis that species cannot be simultaneously tolerant to multiple environmental stress factors (Niinemets et al., 2006). Hence, species in recent forest plots, with higher nutrient availability, are potentially more tolerant to darker conditions. A possible mechanistic explanation for this phenomenon is that on richer soils, plants need to allocate fewer resources to roots and below-ground processes when nutrients are plentiful and can therefore allocate more nutrients to their leaves (Tilman, 1988; Whitehead et al., 2002), resulting in a higher photosynthetic capacity (Field et al., 1986) and allowing plants to grow under lower light levels.

Coomes et al. (2009) also relate nutrient-rich soils to increased plant species richness, because such soils can support both fast-growing light-demanding species and slow-growing species that tolerate deep shade, resulting in a greater range of shade-tolerance niches among species on nutrient-rich soils. This might explain the positive effect of Olsen P concentration on both species richness and Shannon-diversity that we found. For these biodiversity measures, land-use history was however not important, which suggests that the interactive effects of land-use history and light-availability on the herb cover might additionally be related to other differences (other than nutrient availability) between ancient and recent forests. One such difference is the overall lower shade-casting ability in recent forest plots (Appendix N). Hence, it could be that in recent forests, although shade-casting ability increased in general, shade levels have not yet reached threshold levels at which herb cover starts to decline, because of the lower starting levels of shade-casting ability.

The higher overall shade-casting ability values in ancient forests compared to recent forests could also explain the observed interactions between climate warming and land-use history on the herb cover: cover declines in response to warming were only found in recent forests. The forest canopy can buffer plant responses to macroclimate warming (De Frenne, Rodriguez-Sanchez, et al., 2013), with stronger microclimatic cooling effects beneath canopies with higher shade-casting ability (Zellweger et al., 2019). The lower water holding capacity typically found in recent forest soils, in contrast to the well-developed ancient forest soils with thicker O- and A-horizons, could reinforce the susceptibility of the recent forests' herb layer to climate warming (Greiffenhagen et al., 2006; Von Oheimb et al., 2014), as warming decreases water availability through enhanced evapotranspiration (Rind et al., 1990). Moreover, following the optimal resource partitioning theory, in which plants allocate less carbon to roots with increasing nutrient availability, we can expect plants in recent forests to develop less roots and therefore be more sensitive to the drier conditions associated with climate warming (Thornley, 1972; Mausolf et al., 2018).

Reduced light availability because of increased shade-casting ability was also correlated with the overall increase in species evenness. Lower light levels at the forest floor reduces the dominance of fast-growing, competitive, light-demanding species (Honnay et al., 2002). Therefore, evenness can be expected to increase with increasing shade, as the limited availability of light will reduce competitive exclusion by a few dominant light-demanding species, and will favour more shade tolerant species. This shade-induced loss of dominant competitive species with typically high cover values also explains the negative correlation between total herb cover and evenness. Litter quality was never an important predictor in the models, supporting our idea that canopy changes are mainly affecting the herb layer composition through altering light availability (controlled by canopy cover and shade-casting ability) rather than soil conditions (controlled by litter quality).

Across our 19 study regions, neither the community weighted mean (CWM) values for plant height nor specific leaf area (SLA) exhibited a clear directional change between surveys (although plant height would show a general increase when excluding one region, i.e. Warburg reserve (WR)). The investigated functional traits did not show relationships with climate change and increased N deposition. Instead, the functional composition of the herb layer again seemed to be mainly driven by interactions between land-use history and changes in canopy cover (reflecting management changes) and shade-casting ability. In ancient forests, we could relate increased shade to lower plant height and higher specific leaf area (SLA), characteristics associated with the shade tolerant forest specialists that gained importance in ancient forests. As these forest specialists did not increase in recent forests, the absence of clear height and SLA responses to increased shade in these forests is not surprising. Another compositional feature of the herb layer that we assessed was the share of graminoids in the community, as we expected this to be related to SLA changes given the typically lower SLA of graminoids compared to forbs (Vile et al., 2005; Scharfy et al., 2011). The importance of graminoids did however not change significantly across our study regions, and a correlation between graminoid cover proportion and SLA was not confirmed. In contrast to previous studies across spatial gradients at a single point in time (e.g. De Frenne, Graae, et al., 2013), we did not find an increasing importance

564 of taller plants with lower SLA with increasing temperatures, likely because the increased shade levels
565 can attenuate herb layer responses to warming (De Frenne et al., 2015).

566 When resurveying quasi-permanent plots, observer and relocation errors are non-negligible,
567 (Verheyen et al., 2018). However, changes in community properties can still be detected when a
568 sufficiently large number of plots are combined, as in our study. Moreover, Kopecký and Macek (2015)
569 demonstrated that resurveys are robust to uncertainty in original plot location and, when done
570 properly, provide reliable evidence of decadal changes in plant communities. To minimize the
571 observer error, we performed all resurveys with a team of minimum two researchers (Verheyen et al.,
572 2018). Relocation errors might be present in regions where plots were not permanently marked,
573 although for many regions, the available maps and coordinates were supplemented with photographs,
574 schemes and elaborate field descriptions (Appendix A), which should minimize these relocation errors.
575 In addition, whenever possible, we received help from the original surveyor with plot relocation.

576 *Herb covers of ancient and recent forests differ in their sensitivity to warming and N deposition*

577 Increased N deposition was related to decreased herb cover, but only in ancient forests, while stronger
578 warming was related to decreased herb cover only in recent forests (Fig. 4A and 4B). This suggests
579 that herb layers in ancient forests are more sensitive to N deposition, while herb layers in recent
580 forests are more sensitive to warming. As explained above, the stronger response of recent forest
581 herb covers to warming is likely related to the lower microclimate buffering by canopies with lower
582 shade-casting ability, compared to ancient forests. The loss of herb cover with increased N deposition
583 is typically related to the acidifying effect of nitrogen, which is detrimental for the survival of many
584 (herb) species (Tian et al., 2015). This can however not explain the distinct herb cover responses to N
585 deposition between ancient and recent forests, as pH values were very similar for both land-use
586 categories, and hence we would not expect ancient forest soils to enter the toxic aluminium buffer
587 range (pH_{H2O} < 4.2 sensu Ulrich, 1991) sooner than recent forests. Further (experimental) research is

588 required to understand and confirm the underlying mechanism(s) to these, and our other,
589 observations.

590 *Relating biodiversity and functional changes*

591 Our results suggest that there is nearly no overlap in potential drivers of biodiversity and functional
592 responses of the herb layer. Only the response in total herb cover and species evenness (independent
593 from species richness) share one potential driver, i.e. shade-casting ability. Indeed, we also found
594 negative correlations between these two response variables (total herb cover and species evenness).
595 Over time, the total herb layer cover has declined in the temperate European forests that were
596 studied, and the communities have become more even in the abundance of their species. This
597 suggests that the decline in cover is mainly related to a reduced cover of one or more dominant
598 species, and the overall decreased shade-casting ability seems to be the main potential driver of this
599 observation.

600 **Synthesis**

601 Herb layer community changes in response to environmental alterations differed between ancient
602 and recent forests. These observations confirm our idea that land-use history should not be
603 overlooked in global change studies. Light availability, related to canopy cover and composition, was
604 the most important environmental driver for functional changes and changes in species evenness in
605 the herb layer. Increased shade had the strongest effect on herb layers in ancient forests, where
606 shade-tolerant forest specialists gained importance, while light-demanding competitive species
607 disappeared, resulting in lower cover, higher species evenness, increased specific leaf area and
608 decreased plant height. In recent forests, effects of increased shade on the herb layer were smaller,
609 which we attribute to: (i) higher shade tolerance of light-demanding species when nutrient levels are
610 higher as a legacy of former agricultural use, and (ii) lower initial shade levels in recent forest, which
611 therefore might not yet have reached critical light levels at which communities start responding. On
612 the other hand, the herb layer cover in recent forests was more responsive to increased temperatures,

compared to ancient forests, which we could again relate to canopy properties: communities in ancient forests are likely more buffered to macroclimate warming due to the overall higher shade-casting ability of the canopy.

In general, there seems to be a disconnect between biodiversity and functional responses of the herb layer to environmental changes, and therefore, assessing both types of responses is key to get a more complete understanding of the possible impact of global change on the forest herb layer.

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Author contributions:

LD, KV, MPP and DL conceived of the research idea; all authors were involved in the data collection; LD performed statistical analyses, with assistance from MPP and DL; LD wrote the paper; all authors discussed the results and commented on the manuscript.

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